

THE COMPARATIVE MORPHOLOGY OF THE WINTERACEAE

IV. ANATOMY OF THE NODE AND VASCULARIZATION OF THE LEAF

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With three plates

NODAL ANATOMY

THERE are three basically different types of foliar nodal anatomy in the dicotyledons (Sinnott, 5), viz. unilacunar, trilacunar, and multilacunar. In the primitive trilacunar type, the strands or bundles of foliar vascular tissue are related at the node to three separate and distinct lacunae or interfascicular parts of the hypothetical, cauline, primary vascular cylinder.¹ In the derived unilacunar type, the strand or strands are related to a single "median" lacuna, whereas in the multilacunar one, the strands or bundles of foliar vascular tissue are related to five, seven, or more lacunae.

The nodal anatomy may be constant throughout a family or it may fluctuate in various ways within it. Many families exhibit a mixture of unilacunar and trilacunar nodes or of trilacunar and multilacunar ones, but comparatively few families have the entire range of all three types of nodes. This is due to the fact that most heterogeneous families show a trend of specialization either of reduction from trilacunar to unilacunar or of amplification from trilacunar to multilacunar. These lines of specialization in the nodal anatomy of dicotyledons are not infrequently closely correlated with specializations in other parts of the plants (Bailey and Howard, 1-4), and therefore they are of considerable significance in any discussion concerning natural subdivisions of families.

The nodal anatomy of the Winteraceae is remarkably stereotyped and constant throughout the family. Three foliar bundles are related, *Figs. 1 and 2*, to three lacunae in the vascular cylinder of the stem, i.e. the node is trilacunar in all representatives of the family. The nodal pattern is constant regardless of extreme variations in the size of the leaf, the length and diameter of the petiole, and the character of the lamina. Leaves of *Drimys microphylla* A. C. Sm. and *D. buxifolia* Ridley, a centimeter or less in length, have a similar nodal structure to those of *Bubbia longifolia* A. C. Sm., which may attain a length of 35 centimeters or more. This is particularly significant, since in other dicotyledons extreme reduction in the

¹Recent investigations in palaeobotany and in the study of the ontogeny and comparative anatomy of the vascular plants render essential revaluations and modifications of various established morphological concepts and concomitant revisions and clarifications of terminologies. Owing to existing contradictions and uncertainties in botanical literature, we shall avoid the use of such terms as dictyostele, trace, gap, etc.

size of the leaf not infrequently leads to a reduction of trilacunar nodes to unilacunar ones, just as excessive enlargement of the leaf may lead to an amplification of trilacunar nodes to pentalacunar or multilacunar ones.

VASCULARIZATION OF THE LEAF

Although the nodal anatomy of the Winteraceae is highly stereotyped and stable, the vascularization of the petiole and lamina of the leaf is variable and rather unstable. Simpler types of foliar vascularization tend to occur in most species of *Drimys* and *Pseudowintera*, complex and more highly specialized ones in certain species of *Bubbia*, *Belliolum*, and particularly of *Exospermum* and *Zygogynum*. In the simpler type of vascularization, the three strands of vascular tissue extend outward² through the petiole and for varying distances into the lamina of the leaf, *Figs. 2, 4, and 5*. Sooner or later the lateral ones either diverge laterally or become fused to the median one, which extends outward to the tip of the leaf, *Fig. 6*. In the lower parts of the lamina, the subsidiary veins are detached from the flanks of the lateral strands, *Fig. 4*, whereas in the upper parts of the lamina they branch off from the flanks of the single arc-shaped bundle, *Fig. 6*. In *Drimys* and *Pseudowintera*, there appear to be two trends of specialization of this basic pattern of vascularization. One or more of the strands may divide in the base of the petiole. Such petioles contain 4, 5, or 6 bundles, *Fig. 3*, and in exceptional cases as many as 9 bundles, *Fig. 10*. These bundles may reunite at the base of the lamina, restoring the original number of 3, *Fig. 9*, or they may extend outward for varying distances into the lamina. A second trend of specialization consists of a precocious fusing of the strands to form a more or less conspicuously 3-lobed, arc-shaped bundle, *Fig. 7*, which arises at various levels of the petiole or of the base of the lamina. In certain cases, both types of specialization occur simultaneously, the numerous bundles in the lower part of the petiole fusing to form a more or less continuous arc-shaped strand, *Fig. 8*, in their outward course. The individual bundles vary considerably in size, form, and the amount of cambial activity that occurs within them. The three original strands usually are of comparatively uniform sizes, *Fig. 1*, but the products of their divisions may exhibit markedly different dimensions, *Figs. 3 and 10*. The individual bundles may be broad (tangentially) and shallow (radially), *Fig. 8*, or narrow and deep (due to greater cambial activity), *Fig. 9*.

Although there are a number of distinct patterns of foliar vascularization in *Drimys* and *Pseudowintera*, specific patterns are not stabilized in most cases within species or varieties. Not only do the types of vascularization fluctuate more or less extensively in different collections of the same species or variety, but also in different leaves from the same plant. In the case of the New World (*Wintera*) section of *Drimys*, which we have studied in considerable detail, the range of variability appears to be greater in *Drimys Winteri* varieties *punctata* (Lam.) DC. and *chilensis* (DC.) A. Gray and

²The terminology used is purely descriptive and bears no implications regarding sequences in ontogenetic development, viz. inward or outward development of procambium, xylem, and phloem.

D. granadensis var. *grandiflora* Hieron. than in *D. confertifolia* Phil., *D. Winteri* var. *andina* Reiche, and *D. granadensis* varieties *chiriquiensis* A. C. Sm. and *mexicana* (DC.) A. C. Sm. All of the previously described patterns of foliar vascularization are encountered in leaves from different collections of the first three plants, whereas the more complex types of vascularization have not been found in leaves of the last four. It may be significant, in this connection, that the leaves of the former plants commonly are larger or broader than those of the latter. That the type of vascularization is not determined directly and invariably by the size of the leaf is evidenced, however, by the fact that large leaves may at times have simpler patterns and small leaves complex ones. The length and form of the petiole in relation to the size and form of the lamina are evidently complicating factors in need of future detailed investigation.

In *Drimys* and *Pseudowintera*, division of the three strands to form more than six bundles in the petiole and the base of the lamina is of exceptional occurrence, being confined in the material that we have studied to leaves from certain collections of *Drimys Winteri* varieties *chilensis* and *punctata* and *D. granadensis* var. *grandiflora*. In these specimens there are 7-9 small bundles in the petiole, *Fig. 10*, which frequently tend to become more or less coherent in the basal part of the lamina, *Fig. 8*. The bundles have a normal abaxial orientation of phloem and are arranged in a single symmetrical arc. The tendency for the three strands to form five or more bundles in the petiole is intensified in *Belliolum*, *Bubbia*, *Exospermum*, and *Zygogynum*, and the bundles tend to maintain their individuality in the basal parts of the lamina, i.e. the bundles do not fuse into a more or less coherent arc of vascular tissue, except in certain species of *Bubbia*, e.g. *B. pachyantha* A. C. Sm. (*Brass 4371*).

In *Belliolum*, the more or less numerous bundles of the petiole and midrib, *Fig. 12*, are of normal form and orientation except that the median bundle may at times be conspicuously offset abaxially from a normal position in the arc of bundles, compare *Figs. 10* and *12*. Similar types of vascularization occur in *Bubbia*, but in certain cases three bundles are offset abaxially, *Fig. 14*. The xylem of the offset bundles commonly tends to assume an adaxially indented form as seen in transverse sections. Three of the bundles are offset in the petioles and midrib of *Exospermum Lecarti* v. Tiegh., *Fig. 15*. The median one commonly exhibits an amphicribal form, *Fig. 17*, whereas the xylem of the two lateral ones is indented or horseshoe-shaped. The numerous bundles of the slightly concave arc are of varied forms and orientations. The bundles in the petioles and midrib of *E. stipitatum* (Baill.) v. Tiegh., *Fig. 11*, tend to be associated in pairs that are jacketed in the lamina by sclerenchyma. As shown in *Fig. 13*, one bundle of each pair has an inverted orientation, i.e. the phloem is situated on the adaxial side of the xylem. Similar aberrant types of bundle structure and bundle orientation occur in *Zygogynum*, *Fig. 16*.

The patterns of foliar vascularization fluctuate in *Belliolum*, *Bubbia*, *Exospermum*, and *Zygogynum*, not only in different species, but also within different leaves of the same species. Furthermore, the specific topographical

features, visible in transverse sections, vary more or less at different levels of the petiole and midrib. The ranges of structural variability within species and genera are more or less extensive and may or may not overlap. In the past, most investigators have overlooked or ignored such factors of variability in attempting to differentiate species and genera of dicotyledons by their petiolar structure. Thus, van Tieghem (8) infers a greater stability of structural patterns in the Winteraceae than actually occurs. He states that there are seven bundles in the petioles of *Drimys*, *Pseudowintera*,³ *Belliolum*, and *Bubbia*, three bundles from the median strand and four from the two bifurcating lateral ones. Whereas these bundles have a normal orientation of xylem and phloem, van Tieghem maintains that three of the seven bundles in *Exospermum stipitatum* and *E. Lecarti* have an inverted orientation and are associated in pairs with three normal bundles. Furthermore, according to van Tieghem, there are eight bundles in the petiole of *Zygogynum*, one of which is offset. In *Z. Balansae* v. Tiegh., *Z. bicolor* v. Tiegh., *Z. pomiferum* Baill. and *Z. spathulatum* v. Tiegh., none of these eight bundles divides to form paired bundles, whereas in *Z. Vieillardii* Baill. the offset bundle does so, and in *Z. Baillonii* v. Tiegh. all or several of the upper bundles may do so.

As we have previously shown, there is no such stability in the number and behavior of petiolar bundles in the Winteraceae as hypothesized by van Tieghem. The three foliar strands of *Drimys* and *Pseudowintera* may be unmodified or they may divide to form 4–9 bundles. Furthermore, the three strands or their derivative bundles may fuse to form a single arc-shaped strand. In *Belliolum* and *Bubbia* the petiolar bundles are of variable number and one or more of them may be abaxially offset, as in *Exospermum* and *Zygogynum*. Furthermore, the bundles of the latter genera fluctuate in number, form, and orientation.

Although much more comprehensive collections of the Winteraceae must be studied in detail before attempting to differentiate species and genera upon the basis of their petiolar structure, the available evidence indicates that there are fundamentally significant trends of structural specialization within the family. Two of these trends of specialization are discernible in *Drimys*, leading (1) toward division of the three foliar strands to form more or less numerous derivative bundles, and (2) toward the fusion of bundles to form a single arc-shaped vascular strand. The former trend of specialization is intensified in *Belliolum* and *Bubbia* and attains its climax in *Exospermum* and *Zygogynum*, where the most complex and highly modified types of vascularization occur. It is significant in this connection, however, that although the range of structural variability in the Winteraceae is relatively wide, the vascularization patterns do not overlap or even simulate those that occur in *Illicium*, *Tetracentron*, *Trochodendron*, the Magnoliaceae, Schisandraceae, Degeneriaceae, or Himantandraceae.

The size, form, thickness, and texture of the lamina fluctuate markedly in different representatives of the Winteraceae, as does the venation of

³*Pseudowintera* Dandy, i.e. *Wintera* sensu v. Tiegh., non Murray.

the leaves. *Figs. 21–23* illustrate the venation patterns of *Drimys grana-densis* var. *grandiflora* Hieron. (*Cuatrecasas* 6687), *Bubbia oligocarpa* (Schlecht.) Burt (Schlechter 16470), and *Bubbia pachyantha* A. C. Sm. (*Brass* 4371). The three leaves exhibit such conspicuous differences as to suggest the possibility of differentiating species by characteristic features of their patterns of venation, a problem of much significance to palaeobotanists. The three leaves shown in *Figs. 18–20* are from different collections of the same species, *Drimys piperita* Hook. f. The range of structural variability within this species obviously is nearly as great as that illustrated in *Figs. 21–23*. It is evident, accordingly, that in utilizing the venation of leaves for taxonomic purposes, it is essential to examine numerous collections from different parts of the range of each species, viz. from as different environments as possible.

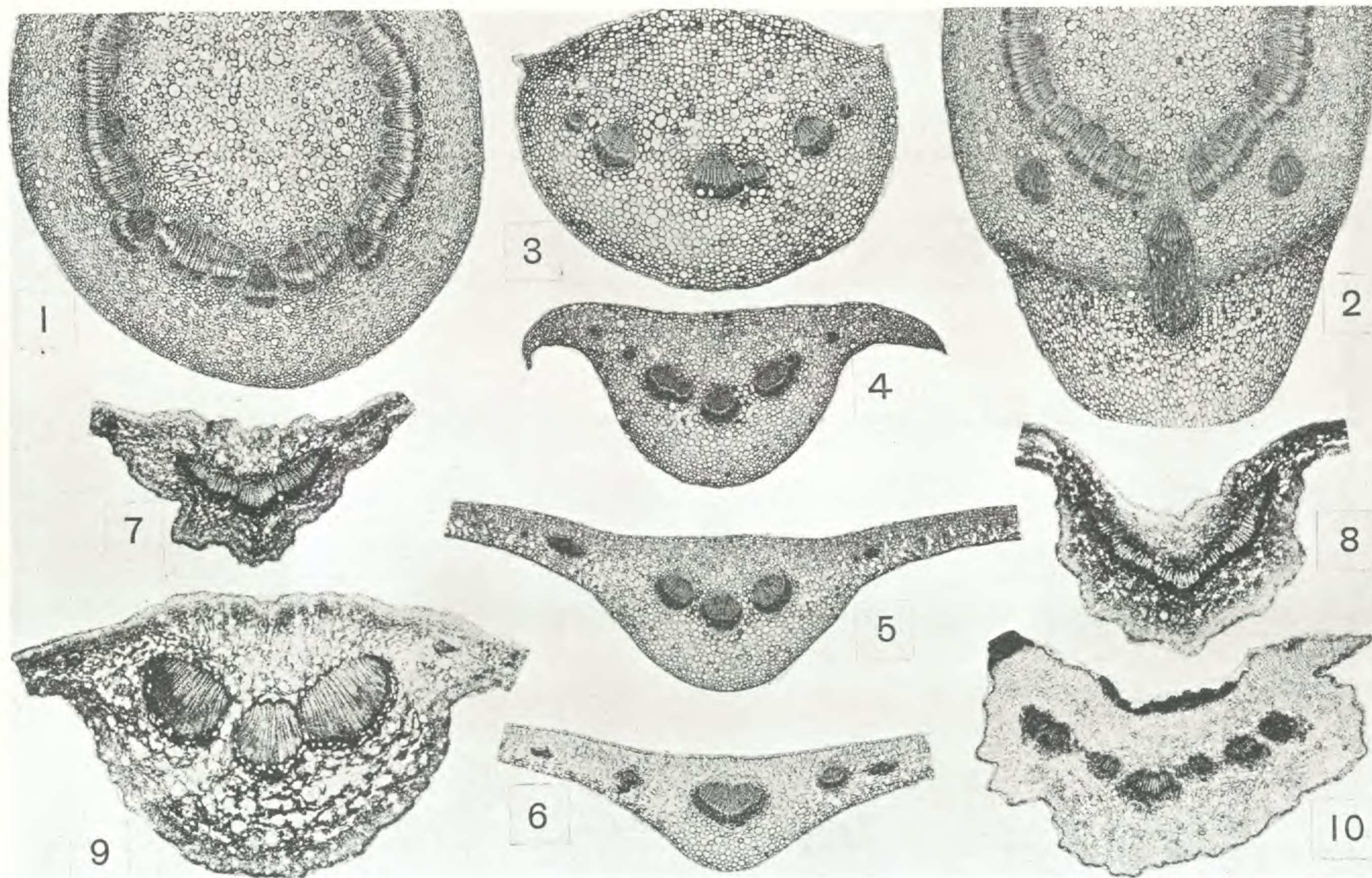
Through the collaboration of our colleague, Dr. Smith (6, 7), we have had the opportunity of studying numerous identified collections of various representatives of the Winteraceae. It is evident from analyses of this material that the ranges of structural variability differ in different genera, species, and varieties. They may or may not overlap. Thus, the terminal veinlets of the New World (*Wintera*) section of *Drimys* are typically slender, *Fig. 21*. The coarser types of venation, *Figs. 20* and *23*, apparently do not occur in the New World representatives of the Winteraceae. This is significant in view of the diverse environments in which these plants grow in Mexico, Central America, South America, and Juan Fernandez, and indicates that genetic as well as environmental factors must be assessed in studying foliar venation. Less slender types of terminal veinlets are predominant in Old World representatives of the Winteraceae; the coarser types of venation, *Figs. 20* and *23*, having been encountered commonly in *Bubbia* and *Zygogynum* and less frequently in *Belliolum* and the *Tasmannia* section of *Drimys*.

The more conspicuous fluctuations in the diameter of the veins and veinlets, illustrated in *Figs. 18–23*, are determined largely by variations in the amount of sclerenchymatous tissue that jackets the vascular bundles. In the coarser-veined types of leaves, there is a massive development of sclerenchyma about the bundles of the midrib, the veins, and the terminal veinlets. In the slender-veined leaves of the *Wintera* section of *Drimys*, on the contrary, much less sclerenchyma is formed about the bundles of the midrib and veins, and the terminal veinlets commonly are devoid of sclerenchymatous jackets. Among the Old World representatives of the Winteraceae, such veinlets are of infrequent and sporadic occurrence, having been encountered by us only in certain collections of *Drimys insipida*, *D. lanceolata*, *D. piperita*, *D. stipitata*, *Pseudowintera axillaris* var. *colorata*, *Zygogynum pomiferum*, and *Z. spathulatum*.

It should be emphasized, in conclusion, that there is a conspicuous trend of specialization in *Belliolum*, *Bubbia*, *Exospermum*, and *Zygogynum* leading toward intense sclerification of both vegetative and floral organs. The formation of very coarsely veined leaves appears to be a concomitant of this general trend of structural specialization.

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